

Distribution of Juvenile and Subadult Kemp's Ridley Turtles: Preliminary Results from the 1984-1987 Surveys

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*Juvenile life stages of Kemp's ridley turtle (*Lepidochelys kempi*) are widely distributed throughout the coastal waters of the United States from Texas to New England. For the most part, these individuals could be described as post-pelagic "yearlings" that have left the pelagic habitat for the nearshore benthic habitat to forage primarily on motile forms of crustaceans such as portunid crabs. Historical records from the turn of the century characterize the ridley as a common inhabitant of North Carolina bays and estuaries. Kemp's ridley was the second most abundant sea turtle caught in the Cedar Key, Fla., turtle fishery, but this may reflect fisherman bias for the green turtle.*

Following the drastic decline in the size of the Rancho Nuevo, Mexico, rookery over the past four decades, a similar decrease in numbers of juveniles and subadults in our coastal waters would be expected. Early surveys conducted in the northern Gulf of Mexico substantiated that this was the case. However, occurrences of unusual numbers of juvenile Kemp's ridleys captured in relatively restricted areas have been recently reported in Louisiana, Alabama and, to some extent, in northwest Florida. In two cases, the most significant biological factor associated with these frequent captures was the abundance of portunid crabs. In some cases, cold-stunned turtles were obtained from both coasts of Florida following episodes of severe winter temperatures.

Records of Kemp's ridleys collected or observed, weighed and measured, and tagged and released are presented. Anecdotal information from various informants and miscellaneous observations are summarized.

The early life history stages of Kemp's ridley turtle (*Lepidochelys kempi*) have not received as much attention by biologists as have studies of the older, reproductively active adults. This was probably due to their small size, reduced numbers and cryptic habits in the extensive marine environment of the Gulf of Mexico and North Atlantic, and was compounded by their being frequently misidentified (Brongersma, 1982). However, adults, as well as juveniles, were relatively common years ago and well known to the trawlermen of the Gulf of Mexico (Liner, 1954; Carr, 1977). After the nesting beach at Rancho Nuevo, Mexico was discovered by scientists in 1961 (Hildebrand, 1982), ridleys became highly visible and relatively accessible to biologists at the rookery. That was the situation until their numbers declined to the low levels reported today (Márquez, Villanueva and Burchfield, 1989). Before their numbers decreased to present levels, tagging studies conducted by Mexican biologists at Rancho Nuevo revealed that females returned to crab-rich foraging grounds either south of the rookery in the Tabasco-Campeche Bay region or north, primarily off the Louisiana coast, after the nesting season (Chávez, 1969; Pritchard and Márquez, 1973; Márquez, 1984). It was also determined that the majority of tag returns came from shrimp fishermen trawling in those two areas (Márquez, 1984; National Marine Fisheries Service, 1987).

Nothing is known about the distribution, or even the occurrence, of Kemp's ridley hatchlings in the pelagic stage in the Gulf of Mexico. A few are sometimes observed swimming in the surf zone off Padre Island, Tex., and some have been tossed up on the beaches of Mustang Island, Tex. during storms (Anthony Amos, The University of Texas, and National Park Service personnel, Padre Island National Seashore, personal communication). In either case, the littoral zone, with its attendant predators, is clearly not the appropriate habitat of these young turtles. Paradoxically, the smallest post-hatchlings recorded were two specimens found in the Atlantic (Schmidt and Dunn, 1917; Deraniyagala, 1939). One was from the Azores and the other from an unknown locality identified only as "United States."

The juvenile life history stage, not including the hatchlings or the post-hatchling pelagic stage (Carr, 1986), is best described as the post-pelagic or coastal benthic stage that feeds primarily on crustaceans such as portunid crabs, bivalves, and a variety of other invertebrates (Dobie, Ogren and Fitzpatrick, 1961). This developmental stage is widely distributed throughout the Gulf of Mexico and northward along the Atlantic coast from Florida to New England. Kemp's ridley has also been recorded from Bermuda (Mowbray and Caldwell, 1958), but nowhere else in the western North Atlantic, and that includes the Bahamas and Antilles (Carr, 1980).

In the eastern Atlantic, Kemp's ridleys include a wide range of size classes, from small post-hatchlings to larger juveniles with carapace lengths from 10 to 25 cm (Carr, 1980). In the western Atlantic only one adult size individual (66 cm) has been captured at Cape Canaveral, Fla. (Henwood and Ogren, 1987). Other records showed that Kemp's ridleys from the western Atlantic ranged in size from 20 to *circa* 60 cm carapace length (Table 1). Several more adult

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Table 1. Size distribution of Kemp's ridley turtles from the Atlantic coast.

Straight line ^a carapace length, centimeters		n ^b	Locality	Date	Source
Mean	Range				
30	27-33	7	Cape Cod Bay, Mass.	Nov. 1978	Lazell (1980)
35.6	26.5 - 43	7	Sandy Hook Bay / New York Bight	Jun. - Nov. 1973-1975	Tom Azarovitz (unpublished)
*41	27-62	21	Chesapeake Bay, Va.	May - Nov. 1979-1981	Lutcavage and Musick (1985)
34.8	20.3 - 57.2	21	S.C. and Ga. coastal zones	Jun. - Nov. 1978-1983	Henwood and Ogren (1987)
38.6	24.1 - 66	40	Cape Canaveral, Fla.	Dec. - Mar. 1978-1984	Henwood and Ogren (1987)

^aExcept as noted by asterisk (*) indicating curved measurement. Curved carapace length measurements are approximately 2 centimeters greater than straight line measurements.

^b Sample size.

size individuals have been found stranded on Atlantic coast beaches of South Carolina, Georgia and Florida (Barbara Schroeder, National Marine Fisheries Service, personal communication), and René Márquez (Instituto Nacional de la Pesca, personal communication) reported the capture of two adult females offshore the Dry Tortugas and the upper Florida Keys. With the discovery of the rookery at Rancho Nuevo, a postulated old world origin for these individuals was laid to rest (Brongersma, 1972). However, the fate of these turtles in the North Atlantic remains undetermined. Some obviously die from exposure to low temperatures if they venture too far north (Lazell, 1980; Meylan and Sadove, 1986). Whether all are lost never to enter the breeding population, or whether they return to the Gulf of Mexico to mature, breed or both is not known.

Historical records from the turn of the century characterize juvenile Kemp's ridleys as common inhabitants of North Carolina bays and sounds (Coker, 1906). Kemp's ridley was the second most abundant sea turtle caught in the Cedar Key, Fla., turtle fishery (Carr and Caldwell, 1956). However, this might not reflect the natural conditions concerning the species' abundance at that time because of the fishermen's bias for the green turtle (*Chelonia mydas*). Elsewhere in the United States, unusual numbers of small Kemp's ridleys were found cold-stunned in Vineyard Sound, Mass., and were reported to be a common inhabitant of New York Harbor (Babcock, 1930; Carr, 1980).

The nesting population of Kemp's ridley at Rancho Nuevo was first observed by biologists in the early 1960s when it was determined that numbers of nesters estimated from a single *arribada* in 1947 had been reduced by more than 92 percent (Márquez, 1984). A corresponding decrease in the number of hatchlings produced would be expected, and the number that survived the pelagic stage and entered the coastal benthic population as juveniles would therefore also be lowered. This decline was the result of systematic and intensive egg harvest over a period of many years (Hildebrand, 1982), in addition to other natural causes and continuing incidental catch primarily by shrimp trawlers elsewhere in the species range.

During the last two decades, increasing beach protection provided by the Mexican government and a very successful hatchery program operated by Mexican and American biologists at Rancho Nuevo produced an average of 20,000 hatchlings annually the first decade and 50,000 annually thereafter (Márquez, 1984). This can be expected to have resulted in a major demographic change for Kemp's ridley in the Gulf of Mexico, and possibly the western Atlantic region as well. However, the adult population continued to decline steadily during 1978 to 1985 (Frazer, 1986), and only about 600 females nested at Rancho Nuevo in 1986 (Richard Byles, U.S. Fish and Wildlife Service, personal communication; National Marine Fisheries Service, 1987). Observations or incidental captures of adult ridleys at sea have become rare events. Conversely, juveniles in the post-pelagic benthic stages are now commonly found at various localities in coastal waters from Texas to New England, probably as a result of the protection afforded the nesters and nests at Rancho Nuevo for two decades.

The following account presents capture, tagging and recapture results and size distribution data obtained in recent years. These studies are part of the long-term effort to determine migratory patterns, seasonal occurrence and distribution and growth of foraging populations of juvenile sea turtles in coastal waters. They provide support for the overview I will give of the early life history of Kemp's ridley.

Table 2. Size distribution of Kemp's ridley turtles from the northern Gulf of Mexico.

Straight line carapace length, centimeters		n ^a	Locality	Date	Source
Mean	Range				
53.5	38-64	72	Cedar Key, Fla.	Apr. - Nov. 1955	Carr and Caldwell (1956)
45.9	35.5-57	36	Cedar Key, Fla.	May - Nov. 1984 - 1987	NMFS ^b
35.5	20.3-55.9	30	Apalachicola - Apalachee Bays, Fla.	Mar. - Jan. 1970 - 1985	Jack Rudloe (unpublished) NMFS
37.4	20.3-53	53	Apalachicola - Apalachee Bays, Fla.	Jan. - Dec. 1985 - 1987	Jack Rudloe (unpublished) NMFS
31	25.8-39	7	Mississippi Sound & coastal zone, Ala.	Feb. - Oct. 1966-1983	Carr (1980) NMFS
23.7	21.6-26.3	5	Terrebonne and Caillou Bays, La.	Jun. 1984	NMFS
32.3	20.3-45.7	61	Sea Rim State Park, Tex.	Apr. - Nov. 1983 - 1985	Texas Parks & Wildlife Dept. STSSN ^c
31	24.1-39.8	6	La. coastal zone and eastern Tex.	Mar. - Nov. 1978	NMFS

^a Sample size.
^b National Marine Fisheries Service.
^c Sea Turtle Stranding and Salvage Network.

Capture, Tagging and Recapture

At-sea capture of sea turtles continues to be the most important and productive source of information from which we at the National Marine Fisheries Service, Panama City, Fla., Laboratory ascertain the distribution and abundance of sea turtles in coastal waters. This is especially true when a turtle biologist or a similarly trained person is directly involved in collecting or handling the turtles and in recording the species identification and morphometrics. In addition, references dealing with significant numbers of juveniles turtles and meristic data have been selected from other sources to complement our limited data (Tables 1 and 2).

In general, most of our sea turtle capture efforts in the southeast region of the United States are either by active fishing gear, such as trawls and strike gill nets, or more passive methods such as turtle entanglement nets. The primary objective of capturing turtles is to tag and release them. In certain areas along the coasts of the Gulf of Mexico and Atlantic Ocean, turtles are sometimes captured in pound nets, by hook and line, and fortuitously when they are immobilized by cold temperatures (Ogren and McVea, 1982; Ehrhart, 1983). Some stranding records also were included in the size distribution examples discussed, but most captures were made by shrimp trawls.

Juvenile Kemp's ridleys are not the only species collected during our capture efforts. Adult and subadult loggerheads (*Caretta caretta*) dominate the catch on the Atlantic coast, and juvenile green turtles, although less abundant in our catches than are loggerheads and Kemp's ridleys, are found in both areas in the Gulf and Atlantic. Other areas along the Gulf Coast of Florida south of Cedar Key are reported to have significant numbers of juvenile green turtles (Paul Raymond, National Marine Fisheries Service, personal communication). An expansion of our netting activities at Cedar Key is being planned to include sampling in the Homosassa, Fla., area. New netting methods are being developed for sampling Corrigan and Waccasassa reefs, and sampling areas will be extended to Homosassa, Fla., where conditions appear to be more favorable for capturing subadult green turtles.

Most of the capture and tagging efforts take place along the northwest and east-central coasts of Florida, with considerable seasonable (summer) effort in Winyah Bay, S.C. The most productive method of capture has been with shrimp trawls, but "run-around" gill nets and, more recently, turtle entanglement nets have accounted for an increasing number of captures on the west coast of Florida. More than 600 turtles have been captured, tagged and

Table 3. Recent recaptures of Kemp's ridley turtles along the Atlantic coast.

Tag Code	Date tagged	Capture locality	Capture gear	Date of recapture	Recapture locality	Recapture gear
PPF 541-542	Nov. 29, 1986	Cape Canaveral, Florida	Shrimp trawl	Dec. 13, 1986 & Mar. 23, 1987	Cape Canaveral, Florida	Shrimp trawl
PPF 542-54	Jan. 25, 1987	Cape Canaveral, Florida	Shrimp trawl	Jul. 28, 1987	Glynn County, Georgia	Shrimp trawl

Table 4. Recaptures of Kemp's ridley turtles in the northern Gulf of Mexico.

Tag Code	Date tagged	Capture locality	Capture gear	Date of recapture	Recapture locality	Recapture gear
NNJ 253	Nov. 7, 1984	Mississippi Sound, Biloxi, Miss.	Shrimp trawl	Sept. 16, 1985	Sabine Pass Jetties, Tex.- La. boundary	Shrimp trawl
NNZ 674-907	Jul. 6, 1985	Fidlers Point, Wakulla County, Fla.	Gill net	Jul. 9, 1985	Fidlers Point, Wakulla County, Fla.	Seine net
NNW 701-702	Nov. 18, 1985	1.6 km offshore Shell Island, Bay County, Fla.	Shrimp trawl	Apr. 1986	4.8 km offshore Marsh Island, Iberia Parish, La.	Shrimp trawl
NNZ 219-220	May 31, 1986	Mud Cove, Franklin County, Fla.	Shrimp trawl	Jun. 26, 1986	Mud Cove, Franklin County, Fla.	Shrimp trawl
NNJ 266	Jul. 15, 1986	Mississippi Sound (released 40.3 km offshore Horn Island), Miss.	Shrimp trawl	Aug. 4, 1986	East Deer Island, Mississippi Sound, Miss.	Shrimp trawl
NNJ 267	Jul. 15, 1986	Horn Island, Mississippi Sound, Miss.	Shrimp trawl	Oct. 23, 1986	Dauphin Island, Mississippi Sound, Ala.	Shrimp trawl
NNW 729-730	Jul. 30, 1986	Corrigan Reef, Levy County, Fla.	Turtle net	May 21, 1987	Corrigan Reef, Levy County, Fla.	Turtle net
NNZ 231-232	Dec. 7, 1986	St. George Island, Franklin County, Fla.	Shrimp trawl	Apr. 3, 1987	Alligator Point, Franklin County, Fla.	Shrimp trawl
NNZ 252-253	Apr. 13, 1987	Shell Point, Wakulla County, Fla.	Shrimp trawl	Apr. 16, 1987	Shell Point, Wakulla County, Fla.	Shrimp trawl

released. Of this total, 376 loggerheads, 146 Kemp's ridleys and 22 green turtles have been captured on the Atlantic coast. During 1978 to 1984, approximately 60 juvenile Kemp's ridleys and 20 green turtles were tagged and released on the Atlantic coast (Henwood and Ogren, 1987), and these included a significant number of juvenile and subadult turtles from the coastal waters of the United States offshore the Indian River estuarine system of east-central Florida as reported by Ehrhart (1983). Recent recaptures of Kemp's ridleys on the Atlantic coast are shown in Table 3.

On the west coast of Florida, capture efforts have resulted in the tagging of more than 100 juvenile sea turtles, primarily Kemp's ridleys. The species composition was 110 Kemp's ridleys, 10 green turtles and 7 loggerheads. The capture methods included gill and entanglement nets as well as shrimp trawls. Recent and significant recaptures of Kemp's ridleys in the Gulf of Mexico have been reported (Table 4). One tagged Kemp's ridley was at large at Cedar Key from July 1986 until May 1987, and another migrated eastward from Biloxi, Miss., to Dauphin Island, Ala. Two other tagged Kemp's ridleys were recaptured in Louisiana, a considerable distance westward of their original capture sites at Panama City and Biloxi, respectively.

Figure 1 gives the carapace length-frequency distribution of Kemp's ridleys captured by shrimp trawls during our sampling effort in the northeast Gulf of Mexico from 1984 to 1986.

Overview

Juvenile Kemp's ridley turtles are widely distributed throughout U.S. coastal waters from Maine to Texas. The

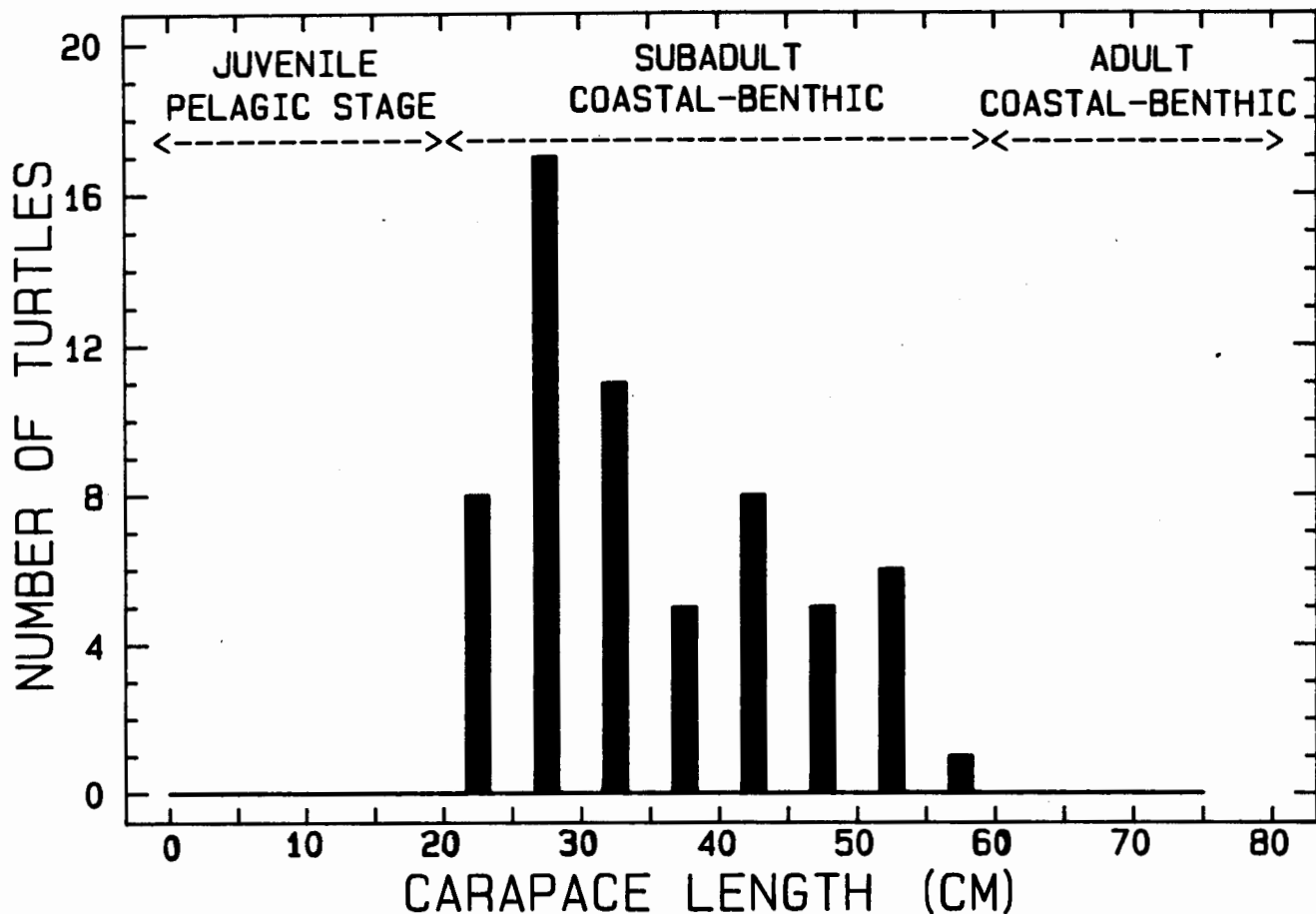


Figure 1. Straight line carapace length-frequency of 61 Kemp's ridley turtles captured in shrimp trawls in the northeastern Gulf of Mexico, 1984-1986.

smallest individuals, ranging in carapace length from 20 to 25 centimeters, are probably post-pelagic stage individuals entering shallow coastal zones of bays, sounds and estuaries (Figure 1). In these developmental habitats, their ecologic niche changes to that of a benthic carnivore. The 20 to 25 cm size class is apparently most numerous in the Gulf of Mexico, giving credence to speculation that the entire life cycle occurs entirely within the Gulf of Mexico for some unknown proportion of the population.

Historically, the smallest post-hatchling Kemp's ridleys were reported only from the New England states and the eastern North Atlantic (Brongersma, 1972; Carr, 1980). However, the ridleys that are found in the Atlantic states to the north and that have a carapace length greater than 25 cm are still relatively small individuals whose movements are most likely mediated by ocean currents. Because of the greater distance from their natal beach, Kemp's ridleys in North Atlantic waters may take a little longer to complete the pelagic development stage than their cohorts in the Gulf of Mexico, and thus they enter the coastal zone at a larger size than those in the Gulf.

Examination of previously published data on sizes of Kemp's ridleys along the U.S. Atlantic coast (Table 1) reinforces earlier comments on the possibility of a north to south increase in size (Carr, 1980), a phenomenon that has also been observed for green turtles (Carr, 1952). This gives support to the idea that the smallest Kemp's ridleys transported out of the Gulf of Mexico are carried by currents northward to New England and then shoreward across the continental shelf via Gulf Stream gyres (Carr, 1980 and 1986). Carr (1980) and others (Lazell, 1980; Meylan, 1986) have proposed this, and the data presented herein agree with such an explanation. Some of these Gulf of Mexico expatriates do not leave the Gulf Stream off New England, but continue their journey to northern Europe and points south in the eastern North Atlantic (Brongersma, 1972 and 1982; Pritchard and Márquez, 1973; Carr, 1980).

There has been considerable debate as to whether or not these Atlantic expatriates survive in the North Atlantic and live long enough to return to the Gulf of Mexico to breed, and conversely as to whether or not they are all doomed waifs, destined either to become cold-stunned in the winter or permanently isolated in the Atlantic (Carr, 1980). Historical records and scientific data strongly suggest that some mortality occurs when young Kemp's ridleys are carried into northern latitudes on either side of the Atlantic and are exposed to the lethal effects of winter temperatures (Lazell, 1980; Meylan and Sadove, 1986). However, some individuals apparently manage to survive, either by being

carried farther downstream to warmer latitudes in the eastern Atlantic, or by some unknown migratory route southward along the coast of the United States to Florida, or both.

In the above case of Atlantic expatriates, our data support the possibility of a seasonal migration south from northern latitudes in the fall, and a subsequent return to northern foraging grounds with the warming of the waters in the spring (Henwood and Ogren, 1987). Other workers studying sea turtle populations along the Atlantic coast have also postulated a seasonal migration among New York Bight, Chesapeake Bay and Florida (Lutcavage and Musick, 1985; Byles, 1989). A similar migratory pattern has been suggested for the loggerhead as well. Otherwise, it is difficult to explain the regular occurrence of significant numbers of viable and healthy sea turtles in northern waters in the warmer months. We have a few Kemp's ridley tag returns from specimens tagged in Florida and recaptured as far north as Chesapeake Bay, and vice versa (Table 3) (Henwood and Ogren, 1987). These could be indicative of what some members of the population do to exploit the crustacean-rich and mollusc-rich foraging grounds north of Florida and to avoid being exposed to the low temperatures that occur for part of the year. Seasonal migrations by other marine poikilotherms are not unusual.

Size distribution of Kemp's ridley along the northern Gulf of Mexico is more or less unremarkable as compared to that along the Atlantic (Table 2). However, some significance should be given to two areas: the smallest Kemp's ridleys found in Gulf coastal waters occur in (1) western Louisiana and eastern Texas and (2) Wakulla and Franklin counties in northwest Florida. These turtles have carapace lengths (20 to 25 cm) that one would expect them to have attained during the time between that when the hatchlings first enter the pelagic stage offshore of the natal beach and the time juveniles enter the coastal benthic stage. However, their precise age is not known. Although we have no documented records of Kemp's ridleys from the pelagic stage, conversations with tuna long-line fishermen indicate that "baby" turtles do occur in the Gulf. In either case, favorable onshore currents exist that could bring them ashore to these two areas east and west of the Mississippi Delta. Wind-driven surface currents west of the Mississippi River and the deeper, more permanent but variable loop current in the eastern Gulf may be the hydrographic features involved in transporting Kemp's ridleys from the pelagic to the coastal benthic habitat. In any event, we have recorded this size class of small Kemp's ridleys as being present in the shallow waters of the upper Texas coast and inshore waters of Louisiana and northwest Florida, and its presence supports the belief that some proportion of the population spends its entire life cycle within the Gulf of Mexico (Table 2, Figure 1).

Other physical and biological factors such as temperature, water depth and food items were studied during the course of our investigations, but the data are scanty and more data will have to be collected before we can discuss their relationships to the distribution of juvenile Kemp's ridleys with any certainty. However, a brief outline will serve to identify some of the more interesting aspects that require further study:

1. Distribution of Kemp's ridleys along the coastal United States is frequently correlated with areas abundant in portunid crabs, their primary prey species (Dobie *et al.*, 1961; Hildebrand, 1982). These areas include blue crab nursery grounds; i.e., shallow seagrass beds and shallow mud bottom bays of coastal marshes, two distinctly different coastal habitats.
2. Localities where numerous juvenile Kemp's ridleys have been reported as captured in trawls since the mid-1970s are:
 - (a) Sabine River offing - Sea Rim State Park, Texas (Jake Dameron, Texas Parks and Wildlife Department, personal communication);
 - (b) Caillou Bay, Terrebonne Parish, Louisiana (Larry H. Ogren, National Marine Fisheries Service, unpublished data); and
 - (c) Big Gulley, east of the Mobile Bay offing, Alabama (Larry H. Ogren, National Marine Fisheries Service, unpublished data; Carr, 1980).

These events, referred to as "jubilees" by coastal Alabamians when applied to other demersal organisms, may have been unusual in that they are thought to be correlated with high concentrations of blue crabs resulting in concentrations of foraging Kemp's ridleys. The displacement of deeper hypoxic water landward by offshore winds and a subsequent shoreward migration of demersal prey species is the most logical explanation for this phenomenon. These physiobiological events are not necessarily regular occurrences but appear to be episodic in nature (May, 1973; Renaud, 1986).

3. The shallow coastal waters of the Gulf of Mexico serve as the foraging habitat for Kemp's ridleys throughout the year. A seasonal offshore movement in response to low water temperatures is suggested. Three juvenile Kemp's ridleys, 20.0 to 47.5 cm in carapace length, were captured by trawling at depths of 21 to 29 meters during late winter to early spring (January to April) off Apalachicola Bay, Fla. Data on such offshore movement to deeper and warmer water for northern Gulf Kemp's ridleys are scanty, however.

On the Atlantic coast, coastal habitats as far north as Massachusetts are utilized by Kemp's ridleys during summer. The New England Kemp's ridleys frequently succumb to cold temperatures during November and December. Other Kemp's ridleys occurring south of Cape Cod may survive and some may migrate south to Florida to overwinter (Ogren and McVea, 1982; Henwood and Ogren, 1987).

4. Preliminary findings, albeit qualitative, suggest that the northern Gulf coast from Port Aransas, Tex., to Cedar Key, Fla., is the foraging habitat for subadult Kemp's ridleys. Historically, Florida Bay in southeastern Florida was identified as subadult Kemp's ridley habitat, but recent information is lacking in this regard (Carr, 1952). On the southeast coast of the U.S., Kemp's ridleys are apparently common from Cape Canaveral north to Chesapeake Bay, but they are less abundant than in the Gulf. They are found inshore only during spring, summer and fall north of a latitude *circa* 20°N. During winter they apparently migrate either south or offshore to warmer waters and are apparently much more abundant at Cape Canaveral during December to February than at any other time.
5. Turtle size and water depth relationships were observed for a large sample (n = 79) of juvenile Kemp's ridleys from northwest Florida. Most (91 percent) were captured in depths 6.1 meters or less, but all of the Kemp's ridleys less than 25 cm in carapace length, except one, were collected from depths 0.9 meters or less. This supports the belief that their exploitable foraging habitat is restricted to shallow depths because of the feeding energetics of these small individuals; i.e., their high specific metabolic rate and an aerobic diving strategy (Peter Lutz, University of Miami, personal communication).
6. Kemp's ridley captures were associated with a variety of substrates and bottom types including mud, sand, oyster shell and turtle grass (*Thalassia*). No preference was indicated except when associated with portunid crab distribution (see above).

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